

Glyphosate-Resistant Horseweed (*Conyza canadensis*) in Mississippi¹

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Abstract: Survival of horseweed in several glyphosate-tolerant cotton and soybean fields treated with glyphosate at recommended rates preplant and postemergence was observed in Mississippi and Tennessee in 2001 and 2002. Plants originating from seed collected from fields where horseweed escapes occurred in 2002 were grown in the greenhouse to the 5-leaf, 13- to 15-leaf, and 25- to 30-leaf growth stages and treated with the isopropylamine salt of glyphosate at 0, 0.025, 0.05, 0.1, 0.21, 0.42, 0.84, 1.68, 3.36, 6.72, and 13.44 kg ae/ha to determine if resistance to glyphosate existed in any biotype. All biotypes exhibited an 8- to 12-fold level of resistance to glyphosate when compared with a susceptible biotype. One resistant biotype from Mississippi was two- to fourfold more resistant than other resistant biotypes. Growth stage had little effect on level of glyphosate resistance. The glyphosate rate required to reduce biomass of glyphosate-resistant horseweed by 50% (GR₅₀) increased from 0.14 to 2.2 kg/ha as plant size increased from the 5-leaf to 25- to 30-leaf growth stage. The GR₅₀ rate for the susceptible biotype increased from 0.02 to 0.2 kg/ha glyphosate. These results demonstrate that the difficult-to-control biotypes were resistant to glyphosate, that resistant biotypes could survive glyphosate rates of up to 6.72 kg/ha, and that plant size affected both resistant and susceptible biotypes in a similar manner.

Nomenclature: Glyphosate; horseweed, *Conyza canadensis* (L.) Cronq. #³ ERICA; cotton, *Gossypium hirsutum* L.; soybean, *Glycine max* (L.) Merr.

Additional index words: Biomass reduction, glyphosate resistance, herbicide resistance, herbicide tolerance, weed resistance.

Abbreviations: DAT, day after treatment; POST, postemergence; WAT, week after treatment.

INTRODUCTION

Glyphosate has provided broad-spectrum postemergence (POST) control of annual and perennial broadleaf, grass, and sedge weeds for over 20 yr. In recent years, glyphosate has been used to control weeds in glyphosate-tolerant crops such as corn (*Zea mays* L.), cotton, and soybean (Askew and Wilcut 1999; Ateh and Harvey 1999; Faircloth et al. 2001; Johnson et al. 2000; Reddy and Whiting 2000). Glyphosate is also used to control existing vegetation in pastures and roadsides (Evers 2002; McCarty et al. 1996). In row-crop production systems, glyphosate is frequently used to control vegetation before planting in all crops, after crop emergence in glyphosate-resistant crops, and to control escaped weeds be-

fore crop harvest. However, in recent years, the repetitive use of glyphosate has revealed the existence of resistance to glyphosate for several weed species. Biotypes of goosegrass [*Eleusine indica* (L.) Gaertn.] in Malaysia, rigid ryegrass (*Lolium rigidum* Gaud.) in Australia, and horseweed in the United States have developed resistance to glyphosate (Lee and Ngim 2000; Pratley et al. 1999; VanGessel 2001).

Horseweed is an erect summer or winter annual herbaceous weed species that is native to north North America. It is commonly found in cultivated and abandoned fields, roadsides, pastures, utility right-of-ways, and waste areas of the continental United States (SWSS 2003). Individual plants produce vast numbers of seed, the achenes of which are easily spread by wind. Horseweed is often susceptible to common tillage practices of conventional tillage cropping systems; whereas, it often thrives in conservation- or no-tillage systems (Vencill and Banks 1994).

Horseweed is among the top 10 weed species to develop resistance to herbicides (Heap 2003). Widespread involvement of herbicide-resistant populations of horseweed may be due to the cosmopolitan distribution of the

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³ Letters following this symbol are a WSSA-approved computer code from *Composite List of Weeds*, Revised 1989. Available only on computer disk from WSSA, 810 East 10th Street, Lawrence, KS 66044-8897.

species, the ability to prosper in a wide range of environments (crop to noncropland systems), the evolution of reduced tillage practices, or vast seed production potential. Biotypes of horseweed resistant to triazine, sulfonyleurea, glyphosate, and bipyridylum herbicides have been found worldwide (Gadamski et al. 2000; Heap 2003; Mueller et al. 2003; Smisek et al. 1998). Biotypes with 4- to 12-fold resistance to glyphosate have been found in Delaware (VanGessel 2001) and Tennessee (Mueller et al. 2003).

No glyphosate-resistant biotype has been documented to date in Mississippi, a state in which approximately 75 to 90% of the soybean and cotton hectareage, respectively, were planted to glyphosate-resistant varieties in 2002 (Gianessi et al. 2003). However, inconsistent control of horseweed has been reported in several Mississippi fields planted to glyphosate-resistant cotton for several consecutive years.

These studies were conducted to investigate several horseweed biotypes from Mississippi and Tennessee for potential resistance to glyphosate and determine the effect of plant growth stage on glyphosate efficacy for all biotypes investigated.

MATERIALS AND METHODS

Initial Titration Study. Horseweed seeds were collected at maturity from plants that survived at least two 0.84 kg ae/ha applications of glyphosate in three cotton fields and one soybean field in 2002. Two cotton fields were located near Walls, MS, in Desoto County. One was planted to glyphosate-resistant cotton in 2001 and 2002 and glyphosate-resistant soybean in 2000. The second Mississippi cotton field was planted to glyphosate-resistant cotton for three consecutive years (2000 to 2002). The third cotton field, located at the University of Tennessee Milan Experiment Station near Milan, TN, in Gibson County, has been in no-till, glyphosate-resistant cotton each year since 1996. The soybean field was located near Troy, TN, in Obion County and has been in a glyphosate-resistant soybean-conventional corn rotation for six consecutive years since 1997. Seeds from plants in a noncropped site near Cruger, MS, in Holmes County, having no record of glyphosate application during the previous 12 yr, were also collected to serve as biotypes susceptible to glyphosate. The horseweed biotypes will be referred to hereafter as MSDO1 and MSDO2 for the two Mississippi cotton fields, TNGN1 and TNON2 for the Tennessee cotton and soybean fields, and SUSC for the noncropped site. Seeds of each biotype were stored in separate paper bags at 5 C until use.

Seeds of each biotype were planted in the greenhouse in separate 26- by 52- by 6-cm trays containing Jiffy mix potting soil.⁴ Seeds were planted on top of potting soil and subirrigated with distilled water until sufficient number of seed for each biotype germinated. Seedlings in the cotyledon growth stage were transplanted to individual 11-cm-diam pots containing potting soil, resulting in one plant per pot. Plants were grown at 25/15 C (± 3 C) day/night temperature. Natural light was supplemented with light from sodium vapor lamps to provide a 14-h photoperiod. Plants were subirrigated as needed.

Plants in the 10- to 12-leaf growth stage (rosette diameter of 12 to 16 cm) were treated with the isopropylamine salt of glyphosate⁵ at rates of 0, 0.1, 0.21, 0.42, 0.84, 1.68, 3.36, 6.72, and 13.44 kg ae/ha. Spray solutions were applied using an air-pressurized indoor spray chamber equipped with an 8002E flat-fan nozzle calibrated to deliver a spray volume of 190 L/ha at 140 kPa. After spraying, plants were returned to the greenhouse and watered as needed without wetting the foliage. All living aboveground biomass of each plant was clipped at the soil level at 3 wk after treatment (WAT) and dried at 50 C. Shoot dry weight data were expressed as a percent of the nontreated check (i.e., control) for each biotype.

Growth Stage Study. Seeds of the MSDO1, TNGN1, TNON2, and SUSC biotypes were planted in the same manner as described above. Several plantings of each biotype were made so that different sized plants could be treated simultaneously. The MSDO2 biotype was not included because of it having a different growth habit compared with other biotypes. Plants of the MSDO2 biotype bolted at a very young age (~ 21 d after planting); whereas other biotypes maintained a rosette growth habit, and bolting could not be induced regardless of plant size. Plants were grown under similar conditions as described in the initial titration study. For each biotype, plants in the 5-leaf, 13- to 15-leaf, and 25- to 30-leaf growth stage were treated with the isopropylamine salt of glyphosate⁵ at rates of 0, 0.025, 0.05, 0.1, 0.21, 0.42, 0.84, 1.68, 3.36, and 6.72 kg ae/ha. Rosettes of 5-leaf, 13- to 15-leaf, and 25- to 30-leaf plants were 2.5, 9, and 14 cm in diameter, respectively, at time of glyphosate application. Plants were treated in the spray chamber, maintained in the greenhouse, and living aboveground biomass was clipped and dried as described in the initial

⁴ Jiffy Products of America Inc., Batavia, IL 60510.

⁵ Roundup Ultramax[®], Monsanto Company, 800 North Linbergh Boulevard, St. Louis, MO 63167.

Table 1. GR₅₀, level of resistance, and sigmoidal model parameter estimates for glyphosate-resistant (MSDO1, MSDO2, TNGN1, TNON2) and glyphosate-susceptible horseweed biotypes in the initial titration and growth stage studies.

Biotype	GR ₅₀ ^b	Fold level of glyphosate resistance ^c	Model parameters ^a			
			<i>X</i> ₀	<i>a</i>	<i>b</i>	<i>R</i> ²
kg ae/ha						
Initial titration study						
MSDO1	1.37	12	−5.011	642.2	−2.581	0.99
MSDO2, TNGN1, TNON2 ^d	0.94	8	−5.403	1,829	−1.775	0.99
Susceptible	0.11		−0.229	872.8	−0.1207	0.98
Growth stage study, five-leaf plants						
MSDO1	0.22	10	−1.648	2,518	−0.479	0.97
TNGN1, TNON2 ^e	0.14	8	−1.121	5,526	−0.265	0.99
Susceptible	0.02		−0.281	1,553	−0.07	0.99
Growth stage study, 13- to 15-leaf plants						
MSDO1	1.89	11	−10.43	2,404	−3.199	0.99
TNGN1, TNON2 ^e	1.45	8	−7.79	1,437	−2.785	0.97
Susceptible	0.17		−0.068	183.2	−0.246	0.99
Growth stage study, 25- to 30-leaf plants						
MSDO1	2.20	11	−8.114	955.9	−3.563	0.98
TNGN1, TNON2 ^e	1.54	8	−6.762	1,182	−2.662	0.97
Susceptible	0.19		−0.036	176.2	−0.252	0.99

^a Model parameter estimates are for sigmoidal log-logistic model described in the text.

^b GR₅₀ = glyphosate rate required to reduce horseweed dry weight biomass by 50%.

^c Fold level calculated by dividing GR₅₀ value for resistant biotype by GR₅₀ value for susceptible biotype.

^d Average of the MSDO2, TNGN1, and TNON2 biotypes.

^e Average of the TNGN1 and TNON2 biotypes.

titration study. Shoot dry weight data were expressed as a percent of the nontreated check for each biotype by growth stage combination.

Statistical Analyses. Experimental design for both studies was a randomized complete block with four replications of each treatment for each biotype evaluated. Each experiment was conducted three times. No significant experiment effect was observed for either study; therefore, data were pooled across all three experiments of each study. Nonlinear regression analysis and ANOVA were used to determine the effect of glyphosate rate and growth stage on biomass reduction of each horseweed biotype. A sigmoidal log-logistic model (Seber and Wild 1989) was used to relate shoot dry weight reduction as a percent of the nontreated check (*Y*) to glyphosate rate (*x*)

$$Y = \frac{a}{1 + e^{-(x - X_0)/b}} \quad [1]$$

In this equation, *a* is the difference of the upper and lower response limits (asymptotes), *X*₀ is the glyphosate rate that results in a 50% reduction in biomass (GR₅₀), and *b* is the slope of the curve around *X*₀. The level of resistance was determined by dividing the calculated GR₅₀ for the suspected resistant biotype by the GR₅₀ for the susceptible biotype. Pseudo *R*² values were calculated

to assess the goodness of fit for individual regression equations. *R*² values were obtained by subtracting the ratio of the residual sum of squares to the corrected total sum of squares from one. The residual sum of squares was attributed to that variation not explained by the fitted line. The *R*² and residual mean squares were used to determine the goodness of fit to regression models.

RESULTS AND DISCUSSION

Initial Titration Study. Response of each horseweed biotype to increasing glyphosate rate was best fit to a sigmoidal log-logistic model, with *R*² values of 0.98 to 0.99 for the sigmoidal response curve for each biotype (Table 1). There was no significant difference (*P* = 0.394) in the slope of the sigmoidal curves for the MSDO2, TNGN1, and TNON2 biotypes, thus response curves for these three biotypes were averaged (Figure 1). The level of glyphosate resistance was 8- to 12-fold for all four biotypes (MSDO1, MSDO2, TNGN1, and TNON2) when compared with the susceptible biotype (Table 1). The MSDO2, TNGN1, and TNON2 biotypes were 8-fold resistant compared with 12-fold level of resistance for the MSDO1 biotype. Biomass of all four resistant biotypes was 6 to 62% greater at all glyphosate rates except the 13.44 kg/ha rate, where all biotypes were

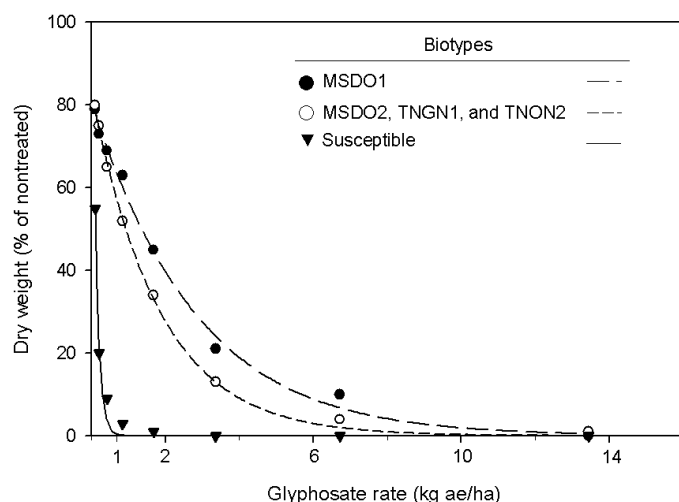


Figure 1. Effect of glyphosate rate on dry weight of four suspected glyphosate-resistant horseweed biotypes (MSDO1, MSDO2, TNGN1, TNON2) and a susceptible biotype 3 wk after treatment. Average of the response curves for MSDO2, TNGN1, and TNON2 biotypes is presented because an *F* test comparison of the slopes of the three curves was not significant at $P = 0.05$. Mean values and sigmoidal functions are plotted, and estimates of sigmoidal model parameters are listed in Table 1.

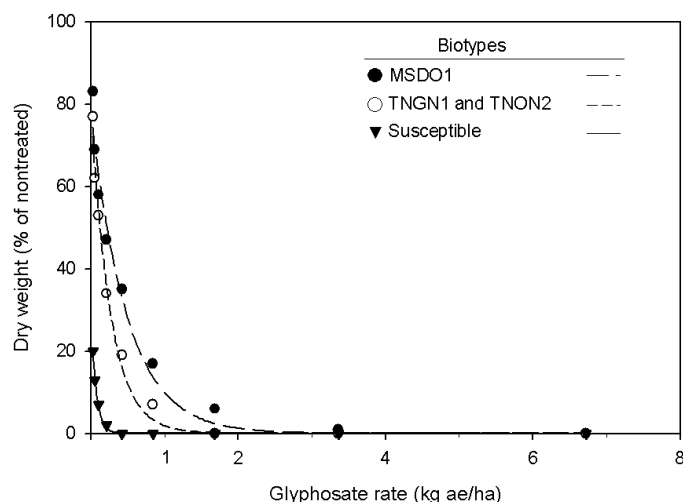


Figure 2. Response of three suspected glyphosate-resistant horseweed biotypes (MSDO1, TNGN1, TNON2) and one susceptible biotype in the five-leaf growth stage to glyphosate rate 3 wk after treatment. Average of the response curves for TNGN1 and TNON2 biotypes is presented because an *F* test comparison of the slopes of the two curves was not significant at the $P = 0.05$ level of significance. Mean values and sigmoidal functions are plotted, and estimates of sigmoidal model parameters are listed in Table 1.

completely controlled. The glyphosate rate required to reduce biomass by 50% (GR_{50}) was 0.94 to 1.37 kg/ha for all four resistant biotypes; whereas, the susceptible biotype required 0.11 kg/ha to achieve 50% biomass reduction. The four resistant biotypes required 3.83 to 5.69 kg/ha glyphosate to reduce biomass by more than 90%, compared with 0.3 kg/ha for the susceptible biotype. Biomass reduction for resistant biotypes was characterized by visual stunting of growth as early as 7 d after treatment (DAT). However, even though biomass of resistant plants was reduced with most glyphosate rates, resistant plants often resumed normal growth with new leaves arising from the rosette center when treated with rates of less than 6.72 kg/ha. Glyphosate at rates greater than 0.84 kg/ha were slightly phytotoxic to resistant biotypes. Shoot apices of resistant plants turned light green to yellow by 5 DAT (data not shown). Most phytotoxicity, however, was transient, with little to no visual phytotoxicity by 10 DAT. Mueller et al. (2003) also reported glyphosate phytotoxicity to be transient, with resistant plants resuming normal growth by 5 to 10 DAT.

Growth Stage Study. The glyphosate-resistant biotypes MSDO1, TNGN1, and TNON2 were 8- to 10-fold resistant to glyphosate when treated at the five-leaf growth stage (Figure 2; Table 1). There was no difference in the level of resistance or slope of the sigmoidal response curves for the TNGN1 and TNON2 biotypes, thus an average response curve for the two biotypes was developed (Figure 2). As in the initial titration study, the

MSDO1 biotype was slightly more resistant (10-fold) than the TNGN1 and TNON2 biotypes (8-fold). The GR_{50} rate for the MSDO1 and average of the TNGN1 and TNON2 biotypes was 0.22 and 0.14 kg/ha glyphosate, compared with 0.02 kg/ha for the susceptible biotype (Table 1). The three resistant biotypes required 0.55 to 0.99 kg/ha glyphosate to reduce biomass by as much as 90%, compared with 0.07 kg/ha for the susceptible biotype.

Plants in the 13- to 15-leaf and 25- to 30-leaf growth stages had 8- to 11-fold level of resistance, regardless of growth stage, for all three resistant biotypes (MSDO1, TNGN1, TNON2) when compared with the susceptible biotype (Figures 3 and 4; Table 1). As in five-leaf plants, the MSDO1 biotype was more resistant (11-fold) than the TNGN1 or TNON2 biotypes (8-fold) at both growth stages (Table 1). An average response curve is presented for the TNGN1 and TNON2 biotypes (Figures 3 and 4) because the level of resistance or slope of response curves was not different for the two biotypes at both growth stages. The GR_{50} rate for the three resistant biotypes increased as growth stage increased, with GR_{50} rates of 1.45 to 1.89 kg/ha glyphosate at the 13- to 15-leaf growth stage to 1.54 to 2.2 kg/ha at the 25- to 30-leaf growth stage (Table 1). The GR_{50} rate for the susceptible biotype also increased from 0.17 kg/ha glyphosate at the 13- to 15-leaf growth stage to 0.19 kg/ha at the 25- to 30-leaf growth stage.

Overall, all four horseweed biotypes evaluated were

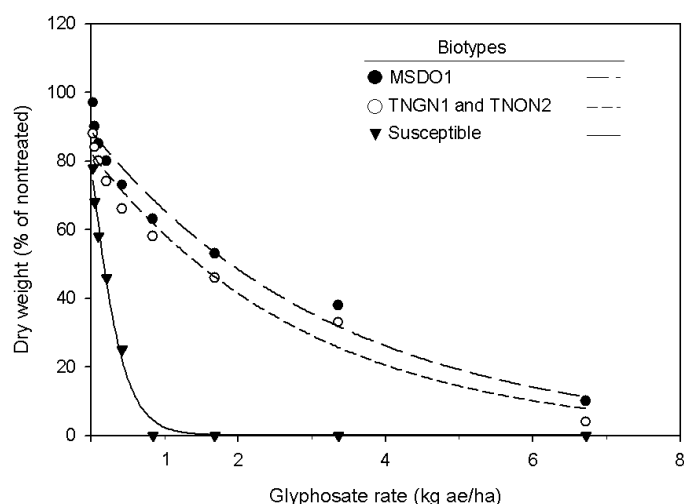


Figure 3. Response of three suspected glyphosate-resistant horseweed biotypes (MSDO1, TNGN1, TNON2) and one susceptible biotype in the 13- to 15-leaf growth stage to glyphosate rate 3 wk after treatment. Average of the response curves for TNGN1 and TNON2 biotypes is presented because an F test comparison of the slopes of the two curves was not significant at the $P = 0.05$ level of significance. Mean values and sigmoidal functions are plotted, and estimates of sigmoidal model parameters are listed in Table 1.

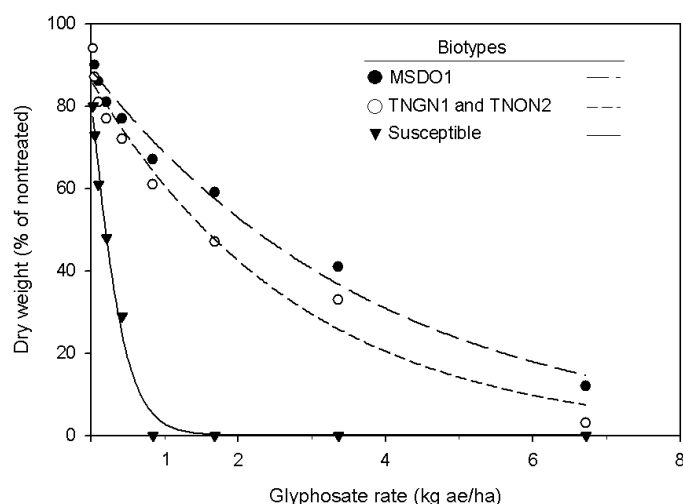


Figure 4. Response of three suspected glyphosate-resistant horseweed biotypes (MSDO1, TNGN1, TNON2) and one susceptible biotype in the 25- to 30-leaf growth stage to glyphosate rate 3 wk after treatment. Average of the response curves for TNGN1 and TNON2 biotypes is presented because an F test comparison of the slopes of the two curves was not significant at the $P = 0.05$ level of significance. Mean values and sigmoidal functions are plotted, and estimates of sigmoidal model parameters are listed in Table 1.

resistant to glyphosate. The level of resistance was 8- to 12-fold depending on biotype, with the MSDO1 biotype being 2- to 4-fold more resistant than the MSDO2, TNGN1, and TNON2 biotypes. These resistance levels are similar to those reported previously. VanGessel (2001) reported 8- to 13-fold resistance for a glyphosate-resistant horseweed biotype from a Delaware soybean field. Similar resistance levels have been reported for other species as well. Populations of rigid ryegrass in Australia and goosegrass in Malaysia have been reported to be 8- to 12-fold resistant to glyphosate (Lee and Ngim 2000; Powles et al. 1998; Pratley et al. 1999).

Growth stage at time of glyphosate application had little effect on level of resistance for all three resistant biotypes evaluated, when compared with the susceptible biotype. The lack of change in the level of resistance was attributable to both the resistant and susceptible biotypes being more tolerant of glyphosate with increasing plant size. The glyphosate rate required to reduce biomass by 50% for resistant and susceptible biotypes increased as growth stage increased. For the three resistant biotypes, the GR_{50} rate ranged from 0.14 to 0.22 kg/ha glyphosate at the smallest growth stage to 1.54 to 2.2 kg/ha at the largest growth stage; whereas, the GR_{50} rate for the susceptible biotype ranged from 0.02 to 0.19 kg/ha between the smallest and largest growth stages.

The similar pattern of glyphosate resistance across biotypes and growth stages suggests similarities in the mechanism(s) responsible for glyphosate resistance in

the resistant biotypes evaluated in this research. In addition, slight to no change in the level of glyphosate resistance across biotype and growth stage sheds light on the possibility that the resistance mechanism may be a genetically altered target site between resistant and susceptible biotypes rather than a mechanism such as reduced absorption, translocation, or metabolism of glyphosate. Feng et al. (1999) found that absorption, translocation, or metabolism of glyphosate was not responsible for glyphosate resistance in rigid ryegrass. The same is true for glyphosate-resistant populations of field bindweed (*Convolvulus arvensis* L.). Westwood et al. (1997) reported that neither absorption nor translocation accounted for differential sensitivity observed in glyphosate-resistant and -susceptible biotypes of field bindweed. The authors also concluded that a cellular or metabolic pathway such as increased shikimate activity may be responsible for the resistance mechanism. Feng et al. (1999) also believed that a similar metabolic pathway such as enhanced shikimate activity might be responsible for glyphosate resistance in rigid ryegrass.

Resistant biotypes survived normal use rates of glyphosate (0.84 kg/ha) with less than 30% biomass reduction in most cases. The above-labeled rates were needed to reduce biomass of glyphosate-resistant horseweed greater than 90%. In the presence of glyphosate-resistant horseweed, weed management strategies other than repetitive POST glyphosate applications are needed. In addition, the wind-dispersal mechanism of glyphosate-re-

sistant seed may hinder the usefulness of rotation of herbicide modes of action for reducing the likelihood of glyphosate-resistant horseweed occurring because seeds are capable of moving long distances and becoming established in new areas.

Future research is needed to determine the mechanism of glyphosate resistance in horseweed. Whether reduced absorption and translocation or increased metabolism of glyphosate is the cause of horseweed resistance is currently being investigated. We will initiate further studies to characterize the pattern of shikimate accumulation, enolpyruvylshikimate phosphate synthase enzyme activity, and genetic diversity of resistant and susceptible biotypes to identify the mechanism responsible for resistance in glyphosate-resistant horseweed.

LITERATURE CITED

- Askew, S. D. and J. W. Wilcut. 1999. Cost and weed management with herbicide programs in glyphosate-resistant cotton (*Gossypium hirsutum*). *Weed Technol.* 13:308–313.
- Ateh, C. M. and R. G. Harvey. 1999. Annual weed control by glyphosate in glyphosate-resistant soybean (*Glycine max*). *Weed Technol.* 13:394–398.
- Evers, G. W. 2002. Herbicides for desiccating dallisgrass (*Paspalum dilatatum*)-bermudagrass (*Cynodon dactylon*) pasture sod prior to overseeding with annual ryegrass (*Lolium multiflorum*). *Weed Technol.* 16:235–238.
- Faircloth, W. H., M. G. Patterson, C. D. Monks, and W. R. Goodman. 2001. Weed management programs for glyphosate-tolerant cotton (*Gossypium hirsutum*). *Weed Technol.* 15:544–551.
- Feng, P.C.C., J. E. Pratley, and J. A. Bohn. 1999. Resistance to glyphosate in *Lolium rigidum*. II. Uptake, translocation, and metabolism. *Weed Sci.* 47: 412–415.
- Gadamski, G., D. Ciarka, J. Gressel, and S. W. Gawronski. 2000. Negative cross-resistance in triazine-resistant biotypes of *Echinochloa crus-galli* and *Conyza canadensis*. *Weed Sci.* 48:176–180.
- Gianessi, L. P., C. S. Silvers, S. Sankula, and J. E. Carpenter. 2003. Plant Biotechnology: Current and Potential Impact for Improving Pest Management in U.S. Agriculture, An Analysis of 40 Case Studies. Washington, DC: National Center for Food and Agricultural Policy: Web page: <http://ncfap.org/40CaseStudies.htm>. Accessed: August 11, 2003.
- Heap, I. 2003. Herbicide Resistant Weeds. Weed Science Society of America: Web page: <http://www.weedscience.org/>. Accessed: August 11, 2003.
- Johnson, W. G., P. R. Bradley, S. E. Hart, M. L. Buesinger, and R. E. Massey. 2000. Efficacy and economics of weed management in glyphosate-resistant corn (*Zea mays*). *Weed Technol.* 14:57–65.
- Lee, L. J. and J. Ngim. 2000. A first report of glyphosate-resistant goosegrass [*Eleusine indica* (L.) Gaertn] in Malaysia. *Pest Manage. Sci.* 56:336–339.
- McCarty, L. B., D. L. Colvin, and J. M. Higgins. 1996. Highbush blackberry (*Rubus argutus*) control in bahiagrass (*Paspalum notatum*). *Weed Technol.* 10:754–761.
- Mueller, T. C., J. H. Massey, R. M. Hayes, C. L. Main, and C. N. Stewart Jr. 2003. Shikimate accumulation in both glyphosate-sensitive and glyphosate-resistant horseweed (*Conyza canadensis* L. Cronq.). *J. Agric. Food Chem.* 51:680–684.
- Powles, S. B., D. F. Lorraine-Colwill, J. J. Dellow, and C. Preston. 1998. Evolved resistance to glyphosate in rigid ryegrass (*Lolium rigidum*) in Australia. *Weed Sci.* 16:604–607.
- Pratley, J., N. Urwin, R. Stanton, P. Baines, J. Broster, K. Cullis, D. Schafer, J. Bohn, and R. Kruger. 1999. Resistance to glyphosate in *Lolium rigidum*. I. Bioevaluation. *Weed Sci.* 47:405–411.
- Reddy, K. N. and K. Whiting. 2000. Weed control and economic comparisons of glyphosate-resistant, sulfonylurea-tolerant, and conventional soybean (*Glycine max*) systems. *Weed Technol.* 14:204–211.
- Seber, G.A.F. and C. J. Wild. 1989. Nonlinear Regression. New York: J. Wiley. 768 p.
- Smisek, A., C. Doucet, M. Jones, and S. Weaver. 1998. Paraquat resistance in horseweed (*Conyza canadensis*) and Virginiana pepperweed (*Lepidium virginicum*) from Essex County, Ontario. *Weed Sci.* 46:200–204.
- [SWSS] Southern Weed Science Society. 2003. Weed Identification Guide. Champaign, IL: Southern Weed Science Society.
- VanGessel, M. J. 2001. Glyphosate-resistant horseweed from Delaware. *Weed Sci.* 49:703–705.
- Vencill, W. K. and P. A. Banks. 1994. Effects of tillage systems and weed management on weed populations in grain sorghum (*Sorghum bicolor*). *Weed Sci.* 42:541–547.
- Westwood, J. H., C. N. Yerkes, F. P. DeGennaro, and S. C. Weller. 1997. Absorption and translocation of glyphosate in tolerant and susceptible biotypes of field bindweed (*Convolvulus arvensis*). *Weed Sci.* 45:658–663.